MALACOLOGIA, 2000, 42(1-2): 75-101

A NEW GENUS AND A NEW SPECIES OF HYDROBIID SNAIL (MOLLUSCA: GASTROPODA: HYDROBIIDAE) FROM EASTERN SPAIN

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ABSTRACT

The identity of *Hauffenia (Neohoratia) gasulli* Boeters, in Gasull, 1981, type material, with shell topotypes and live specimens collected in neighbouring localities, has been established on the basis of shell characters (statistical analysis DFA and Anova). Anatomical studies confirmed its allocation to a new genus, *Tarraconia,* which is only known from the Iberian Peninsula. We present histological data to demonstrate the lack of a seminal receptacle, its function having being transferred to a wide part of the proximal renal oviduct. This character, together with a well-defined data set, including lack of a suboesophageal connective and a gastric caecum, penis size and shape, and a well-developed bursa copulatrix fully protruding from the albumen gland characterise the new genus. *Tarraconia rolani*, n. sp., is also described.

The function of the seminal receptacle having moved to a different part of the genital system, found for the first time among Iberian hydrobiids, has occurred several times in the Hydrobioidea evolution in different families, such as Hydrobiidae, Pyrgulidae, Pomatiopsidae, showing it not to be a useful character to justify suprageneric-level taxa. Detailed anatomical studies are necessary to unravel the obscure phylogenetic relationships of this group of gastropods, which, due to their small size, yield very few diagnostic characters and a high degree of convergence.

Key words: Prosobranchia, Hydrobiidae, *Tarraconia*, anatomy, taxonomy, Iberian Peninsula.

INTRODUCTION

Many of the initial descriptions of hydrobiid species were based only on shell features, mainly because often only empty shells were found. Since shell characters are highly convergent, most early supraspecific assessments have to be reviewed to clear up the existing confusion and to establish a better taxonomic classification (Falniowski & Szarowska, 1995).

Boeter's work (1988) on hydrobiid gastropods from the Iberian Peninsula shows that the problem is still greater among the minute valvatoid Hydrobiidae species, the shells of which are very similar and their anatomy unknown or poorly known. Preliminary studies on Iberian Peninsular hydrobiid snails (Ramos et al., 1992, 1995; Arconada et al., 1996) showed considerable morphological diversity and high endemicity.

The case of *Hauffenia (Neohoratia) gasulli* Boeters, in Gasull, 1981, clearly illustrates the problem. It was described by Boeters in a paper by Gasull (1981) reviewing the terrestrial and freshwater mollusc fauna of Castellón de la Plana Province, eastern Spain. The description and illustrations were based on shell characters, because Gasull only found empty shells. The genus *Hauffenia* Pollonera, 1898, in which species here placed in *Tarraconia* were first included, is widely distributed in freshwater springs on the Balkan Peninsula, Italy, France, Austria, Switzerland, and Slovenia (Bole, 1967, 1970; Boeters, 1973; Bernasconi, 1984; Haase, 1992, 1993; Bodon & Giovanelli, 1994). Described as a subgenus of *Horatia* Bourguignat, 1887, it was treated as a full genus by Bole (1970) after studying the anatomy of the type species, *Hauffenia tellini* Pollonera, 1898. *Neohoratia* Schütt, 1961, was first described as a subgenus of *Horatia,* then ranked as a subgenus of *Hauffenia* by Boeters (1974) and raised to a full genus by Bole & Velkovrh (1986). It is distributed in the Balkans, being represented on the Iberian Peninsula.

In his 1988 paper, Boeters recognised the existence of two genera of valvatoid hydrobiids in Iberia: *Horatia* and *Neohoratia,* and included the latter species as *Neohoratia* (?) *gasulli.* He described differences in the shape

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of both the aperture and the shell in general compared with the other *Neohoratia* species, and pointed out the need for anatomical studies in order to confirm its generic allocation.

Within the framework of the macroproject Fauna Ibérica, only empty shells of the species were found at El Bañador, Altura, Castellón, the type locality and thus far the only known locality. However, many live specimens, with shell characters agreeing with those described by Boeters, have been collected in several springs 3.5 km from the type locality. Once the similarity in shell characters with type material and newly collected topotypes was established using both morphometrical and microsculptural characters, study of the anatomy, confirmed by histological evidence, demonstrated that the combination of character-states in that species does not fit any known genus.

This paper aims to give a detailed account of the species' morphology, describing a new genus and a new species included in the subfamily Hydrobiinae (*sensu* Giusti & Pezzoli, 1984, and Ponder & Warén, 1988).

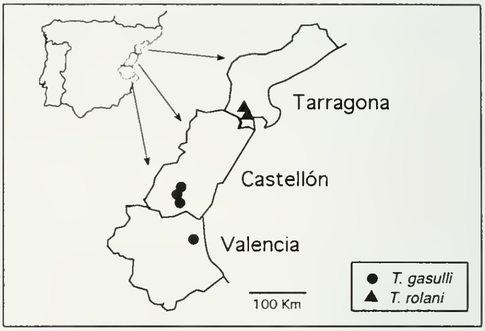

FIG. 1. Map of *Tarraconia gasulli* and *T. rolani* localities.

MATERIAL AND METHODS

Material Studied

Snails collected for this study came from the area marked in Figure 1 in the easternmost part of the Iberian Peninsula. They were collected by hand, either by picking them off the substratum, by washing stones, aquatic vegetation, and dead leaves, or by sieving mud and vegetation.

The stations are listed below consecutively numbered and are referred to in the text by this number. The spring name is followed by biotope type, municipality, province, UTM coordinates, collection date, collector's initials (abbreviations given below). Locality names and UTM are from the official map of the Army Geographical Service. Below each taxon in the following section, locality number, locality name, museum catalogue number, and preservation of specimens is given, except for type material.

01 El Bañador (irrigation ditch), Altura, Castellón, UTM: 30SYK145133. 7/3/1990, Diego Moreno (= D.M.), Jose Miguel Remón (= J.M.R.), Rafael Araujo (= R.A.), and 17/10/1992, D.M. and Nuria Martín (= N.M.).

02 Manantial La Esperanza (spring), Navajas, Castellón, UTM: 30SYK132163, 7/3/1990, R.A., D.M., J.M.R., 15/6/1994, Gloria Tapia (= G.T.), 25/5/1998, Beatriz Arconada (= B.A.).

03 Acequia (irrigation ditch), Navajas, Castellón, UTM: 30SYK133161, 7/3/1990, R.A., D.M. and J.M.R.

04 Fuente de Las Provincias (piped spring), Segorbe, Castellón, UTM: 30SYK151151, 6/10/1990, E.R.

05 Ermita N^a Sra. de la Esperanza (piped spring), Segorbe, Castellón, UTM: 30SYK134162 , 6/10/1990, E.R.

06 Font Nova (spring), Benifaió, Valencia, UTM: 30SYJ513218, 17/3/1994, G.T.

07 Ullal Baltasar (spring), Amposta, Tarragona, UTM: 31TBF969054, 30/3/1990, Jose Bedoya (= J.B.), D.M., R.A., 25/7/1996, Carolina Noreña (= C.N.) and 13/11/1999, B.A.

08 Irrigation ditch on the road from San Carlos de la Rápita to Tortosa, La Carroba, Tarragona UTM: 31TBF943134, 29/3/1990, R.A., D.M. and J.B., 30/9/1990, E.R., 13/3/1999, B.A.

Anatomy

To avoid losing characters through fixation in the newly collected material, such external features as penis shape and colour, snout pigmentation, and presence of calcareous granules at the base of the tentacles, were studied and drawn in the field. To get the best results for anatomical studies, they were relaxed using different narcotic agents and methods (Araujo et al., 1995). On the whole, the best results were obtained by adding a few menthol crystals to the water surface in the container, followed by hot water (60°C, five sec), and then fixing and preserving them in 70% ethanol.

For anatomical studies, specimens were dissected in water on a Petri dish with a black layer of paraffin, wax and coal (Davis, 1967). A Stemi SV8 Zeiss stereomicroscope was used. Anatomical illustrations were based on camera-lucida drawings. Since all anatomical measures were taken from specimens fixed in ethanol, a slight variation in relation to fresh material values was expected, although the effect should be similar in all the study populations.

Radula, protoconchs and opercula were examined with a Philips XL20 Scanning Electron Microscope (SEM). Before the shells were coated with a thin (10–15 nm) gold layer in a Bio-Rad SC515 sputter coating unit, the shell periostracum was removed by immersion in 5% commercial Chlorox (sodium hypochlorite), the time depending on the thickness of the sediment layer covering it. If necessary, a fine paint brush was used to remove any persistent material. The holotype was studied without coating it. Radulae were extracted by digestion of the head with diluted KOH at room temperature. The same method was used to clean the opercula. Both kinds of structures were then rinsed in distilled water and air-dried before mounting on stubs.

Histology

The shells of specimens used for dissections and histological studies were decalcified in 5% aqueous dilution of ethylenediaminetetracetic acid (EDTA). For histology, a male and five females preserved in 70% ethanol were dehydrated in different ethanol series (10 min at both 80%, 90%, and 1 h at both 95%, 100%), transferred to benzyl benzoate, and then embedded in 100% Paraplast Plus. After 14 h in a heater at 59 °C, serial thin sections (4–6 μm) were made with a Leica RM 2045 microtome and hand-stained. We used the Carazzi's hematoxylin-eosin and azan staining methods.

Morphometric Analysis

Eleven shell parameters and six operculum parameters, as shown in Figure 2, were measured. The number of protoconch whorls was counted, beginning at the initial suture (Solem, 1976; Burch, 1982).

Radular central tooth width indicates the distance between the outer cusps of the central tooth.

Bursa copulatrix length does not include its duct. Penis width excludes the penial lobe. Maximum length of prostate, pallial oviduct and ctenidium maximum length were measured without taking curvature into account. Stomach width includes the oesophagus. For the nervous system, RPG ratio was calculated following Davis et al. (1976).

We also calculated the following indices: SL/SW, SL/AL, SW/AW, AL/AW and OL/OW, which seem to describe better the shape of the shell and operculum (abbreviations given below).

All variables (mean value, standard deviation and coefficient of variation) were standardized in order to avoid the effect of the measurement scale. For shell variables, a one-way analysis of variance (ANOVA) was computed for each character to evaluate their contribution to species differences and the post hoc Scheffe's F test was used to examine the statistical significance of the differences between all pairs of means for each level of the factor (population) with a probability level of 5% ($\alpha = 0.05$). The opercular and anatomical variables were compared with a t-test of independent samples.

In order to identify the most important morphological attributes to distinguish directly between species when no anatomical data were available, a discriminant function analysis (DFA) was performed on shell measurements (not ratios). For missing data, casewise option was selected. The significance of the overall discriminatory power of the analysis was tested using the Wilks' *lambda* standard statistic. Standardized coefficients for canonical variables and the canonical correlation (R) were studied to examine each character's contribution in the discriminant function and to analyze the percentage of variance attributed to interspecific variation, respectively. Classification functions were computed for each group (population) to determine, with the highest probability, to which population each case most likely belonged. Cases were assigned to the group having the highest classification score.

Descriptive statistics were obtained using the Statview 4.1 package for Macintosh. DFA was performed using the Statistica 4.1 for Macintosh, Statsoft, Inc., 1984–1994, and Statistica for Windows, Statsoft Inc., 1995, packages.

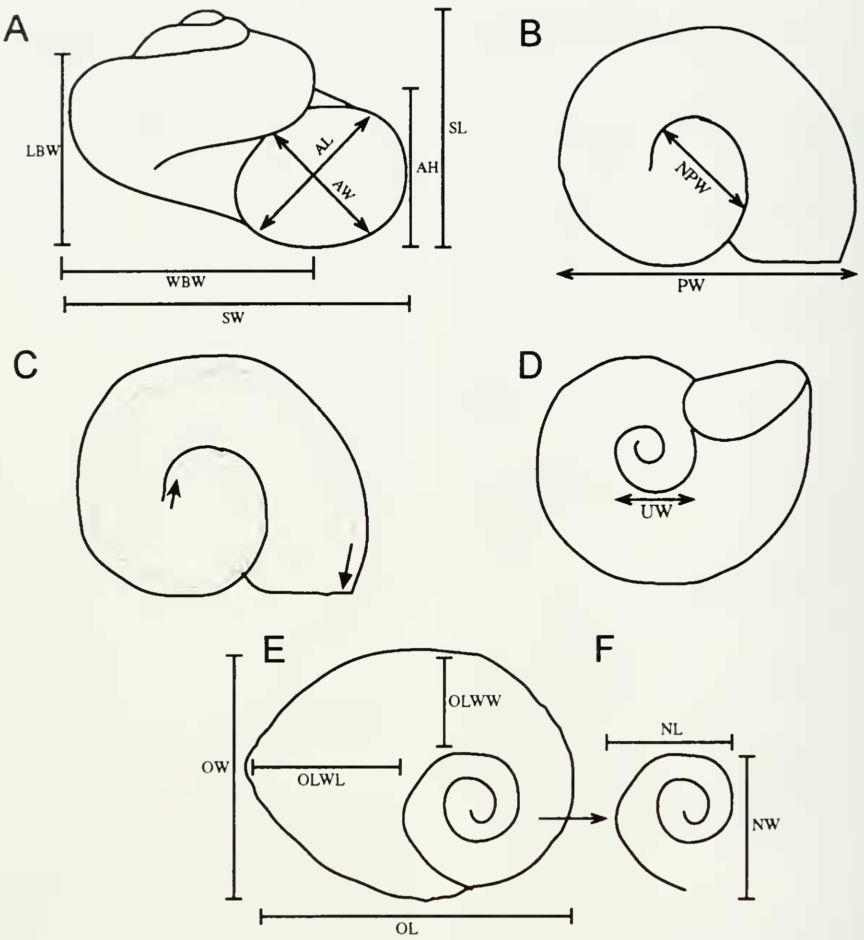

FIG. 2. Shell and operculum measurements. A, B, D. Shell measurements. C. Method employed for counting protoconch whorls. The count begins at initial suture (Solem, 1976; Burch, 1982). E–F. Operculum measurements (see abbreviations in text).

Abbreviations

Shell and Operculum Measurements

- AH Aperture height
- AL Aperture length
- AW Aperture width
- LBW Length of body whorl
- NL Nucleus length of operculum
- NW Nucleus width of operculum
- NSW Number of spire whorls
- OL Operculum length
- OLWL Length of last whorl of operculum
- OLWW Width of last whorl of operculum
- OW Operculum width
- PNW Protoconch nucleus width
- PW Protoconch width
- SL Shell length
- SW Shell width
- WBW Width of body whorl
- WAW Width of the antepenultimate whorl
- WPW Width of the penultimate whorl

Anatomical Measurements

- Ac Anterior chamber of the stomach
- Ag Albumen gland
- Bc Bursa copulatrix
- Ca Egg capsule
- Cc Cerebral commisure
- Cg Capsule gland
- Cgl Left cerebral ganglion
- Cl Columellar muscle
- Co Coiled part of the oviduct
- Ct Ctenidium
- Dbc Duct of the Bursa copulatrix

Dgo	Digestive gland opening
Di	Digestive gland
Int	Intestine
K	Kidney
Lp	Left pleural ganglion
Od	Oviduct
Oes	Oesophagus
Os	Osphradium
Ov	Ovary
P	Penis
Pc	Posterior chamber of the stomach
Po	Pallial oviduct
Pl	Penial lobe
Pr	Prostate
Psc	Pleurosupraoesophageal connective
Pvd	Posterior vas deferens
R	Rectum
Sbo	Suboesophageal ganglion
Spo	Supraoesophageal ganglion
Ss	Style sac
St	Stomach
Sv	Seminal vesicle
T	Testis
Vc	Ventral channel

Collections

The material collected has been deposited in the MNCN collections (catalogue numbers included). One male and one female from Navajas, Manantial La Esperanza have also been deposited in each of the following collections: SMF (9452, 9453) and NNM (312215, 312216). SMF: Senckenberg Museum, Frankfurt; NNM: Natural History Museum in Leiden; MNCN: Museo Nacional de Ciencias Naturales, Madrid; BOE: Boeters' private collection.

SYSTEMATIC DESCRIPTION

Tarraconia Ramos & Arconada, new genus

Type Species

Hauffenia (Neohoratia) gasulli Boeters, in Gasull, 1981

Etymology

Tarraconia is derived from *Hispania Tarraconensis,* an ancient Iberian community that became one of the three provinces into which the Roman Empire divided the Iberian Peninsula in the second century A.D. and which included the current provinces of Tarragona, Castellón and Valencia.

Diagnosis

Shell valvatoid, very small (approx. 1.5 mm in length) and depressed, with 3.5–4 whorls, deep sutures and a wide umbilicus usually carrying an egg capsule; rounded and straight aperture with a characteristic varix behind the outer lip. Operculum has a subcentral nucleus and lacks any outgrowth on the inner surface. Radula typically hydrobiid with a single cusp on each of the basal angles of the central tooth. Right pleural ganglion connected with the supraesophageal ganglion by a long connective; left pleural ganglion and subesophageal ganglion fused. Pallial tentacle absent. Ctenidium well developed, with long lamellae; large osphradium opposite middle of ctenidium. Stomach without caecum; style sac protruding from the intestinal loop that makes a simple coil around the style sac. Rectum U-shaped. Faecal pellets are oval and yellowish. Bursa copulatrix large, fully protruding at the end of the pallial oviduct; renal oviduct very wide near the ventral channel, without seminal receptacles. Penis has a lobe approximately in the middle.

Tarraconia gasulli (Boeters, 1981)

Hauffenia (Neohoratia) gasulli Boeters, in Gasull, 1981 *Neohoratia gasulli* (Boeters): Bole & Velkovrh, 1986 *Neohoratia (?) gasulli* (Boeters): Boeters, 1988

Type Material

Holotype: SMF 256390 one shell by original designation (Figs. 3A–C, 4A, B). Shell measurements in Table 1; paratypes: BOE 952 Gas., SMF 305476 (one shell) and NNM 55554 (one shell). (01) MNCN 15.05/32057 (dried material) (7/3/1990) (Figs. 3D–F) and MNCN 15.05/32059 (dried material) (17/10/1992).

Localities: Manantial La Esperanza (02) MNCN 15.05/32058, 15.05/32060 and 15.05/32066 (dried, ethylic alcohol and frozen material and golden SEM preparation) (Figs. 3G–I, 4C–H); Acequia in Navajas (03) MNCN 15.05/32062 (dried and ethyl alcohol material); Fuente de Las Provincias (04) MNCN 15.05/32064 (ethyl alcohol material and

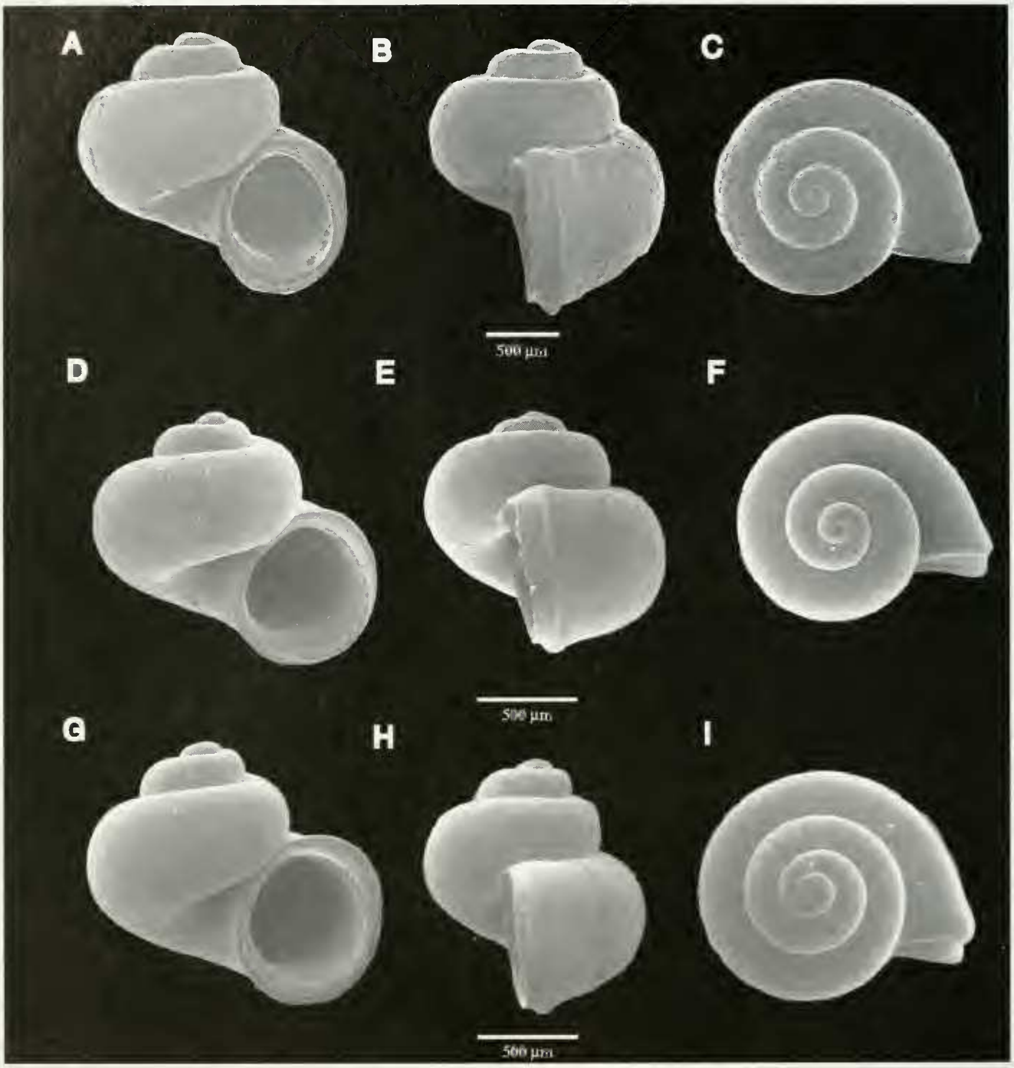

FIG. 3. SEM microphotographs of *Tarraconia gasulli* shells. A–C: Holotype; D–F: from the type locality, El Bañador, Altura, Castellón; G–I: from Manantial La Esperanza, Navajas, Castellón.

golden SEM preparation); Ermita N[a] Sra. de la Esperanza (05) MNCN 15.05/32065 (ethyl alcohol material and golden SEM preparation); Font Nova (06) MNCN 15.05/32063 (ethyl alcohol material).

Type Locality

The type locality is the only place described in Gasull's paper (1981): El Bañador (01), Altura (Castellón).

Morphology

Shell (Figs. 3, 4A–F; Table 1). The shell is dextral, valvatoid, very small (SL: 1.24–1.92; SW: 1.18–1.84), almost as high as wide, thin, whitish, and translucent when fresh, with 3.5–4 whorls. The whorls are rounded, the sutures are deep, and the body whorl occupies 5/6 of total shell length. The aperture adhering to the last whorl is rounded, with slight angularity close to the penultimate whorl. Its outer

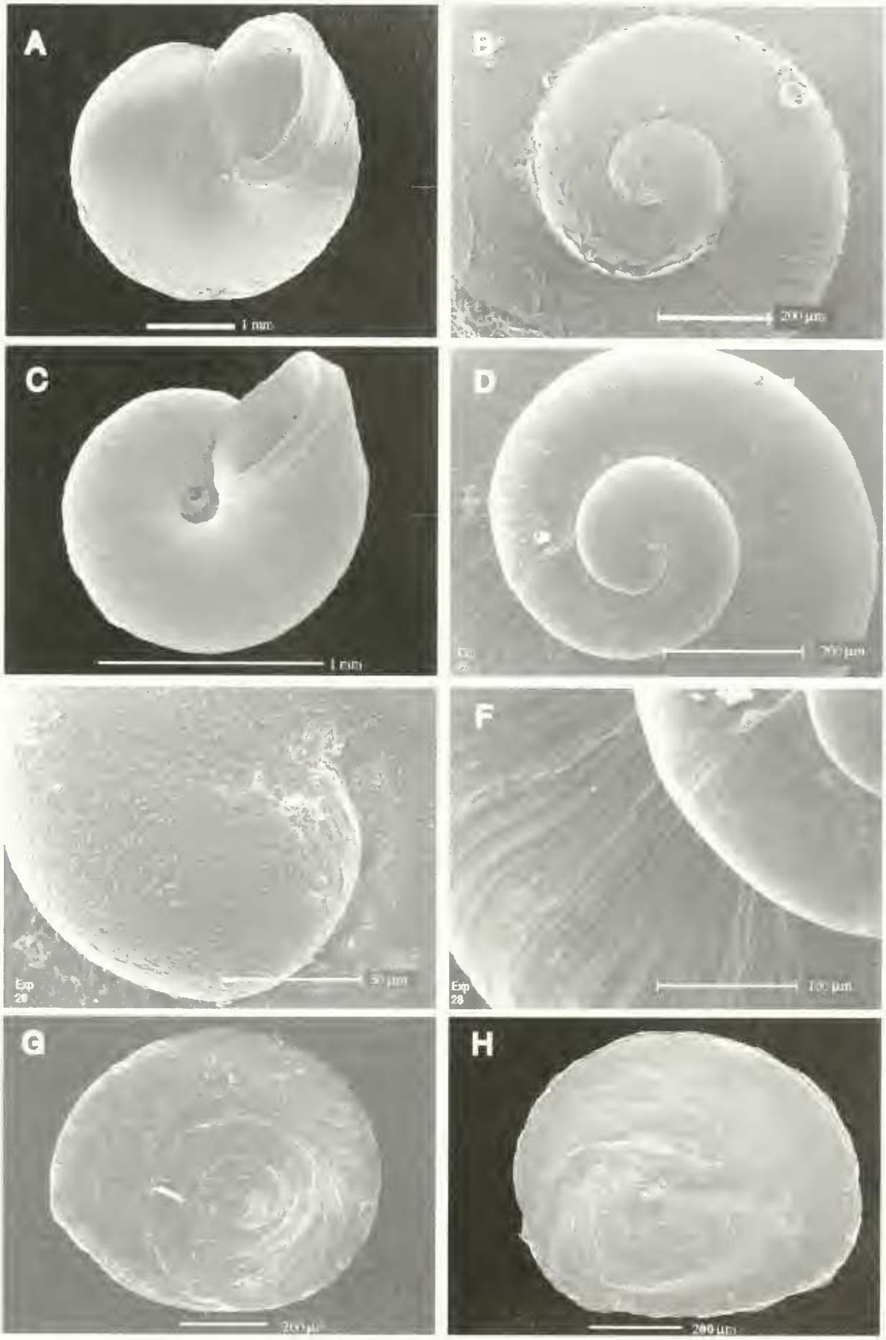

FIG. 4. SEM photomicrographs of *Tarraconia gasulli* shell and opercula. A, B. Holotype. C–H. From Manantial La Esperanza, Navajas, Castellón. A, C. Shell from below (note wide umbilicus and typical varix behind the outer lip); B, D. Protoconch; E. Protoconch sculpture. F. Part of the sculpture of the teleconch. G, H. Outer and inner side of the opercula.

TABLE 1. Shell measurements (in mm) of *Tarraconia gasulli* and *T. rolani*. L = Length, W = Width, SD = Standard Deviation, CV = Coeff. of Variation, * n = 31.

		T. gasulli						*T. rolani*		
	Holotype	El Bañador, Altura (n = 31)			La Esperanza, Navajas (n = 33)			La Carroba (n = 13)		
Variables		Mean	S.D.	C.V.	Mean	S.D.	C.V.	Mean	S.D.	C.V.
SL	1.80	1.58	0.08	0.05	1.61	0.15	0.09	1.38	0.18	0.13
SW	1.80	1.59	0.07	0.04	1.51	0.14	0.09	1.73	0.13	0.08
LBW	1.50	1.34	0.06	0.04	1.32	0.12	0.09	1.11	0.15	0.13
WBW	1.35	1.23	0.05	0.04	1.21	0.09	0.07	1.17	0.12	0.10
AH	1.09	0.89	0.04	0.04	0.88	0.07	0.08	0.88	0.07	0.08
AL	0.83	0.81	0.05	0.06	0.81	0.05	0.07	0.78	0.06	0.08
AW	0.74	0.70	0.03	0.04	0.69	0.05	0.07	0.72	0.07	0.10
NSW	3.75	3.75	0.18	0.05	3.84*	0.22*	0.06*	3.62	0.19	0.05
SL/SW	1.00	1.00	0.04	0.04	1.06	0.06	0.06	0.80	0.08	0.10
SL/AL	2.16	1.96	0.12	0.06	2.00	0.17	0.08	1.77	0.17	0.09
SW/AW	2.43	2.25	0.08	0.04	2.20	0.09	0.04	2.43	0.25	0.10
AL/AW	1.12	1.15	0.04	0.04	1.17	0.08	0.07	1.09	0.05	0.05

lip is straight, parallel to the columella or very slightly inclined backwards, with a characteristic and marked varix behind the outer lip. The umbilicus is very wide, around 0.20 mm, about 1/7 of shell diameter.

The protoconch (Fig. 4B, D, E) is clearly differentiated from the teleoconch (Fig. 4F). The external surface of the protoconch is wrinkled with smoothly pitted sculpture. It has 1.5 whorls. Total width (PW) is approximately 0.32 mm and nucleous width (NPW) approximately 0.15 mm. The teleoconch is smooth, with fine growth lines.

Shell measurements are given in Table 1 both for type locality specimens and those used for anatomical studies (Manantial La Esperanza).

External Body Features. The head is pigmented with black melanin, but the pigment fades towards the snout, which is totally unpigmented, allowing observation of the radular sac due to transparency of the epithelium. There are characteristic orange spots around the eyes (Fig. 8C). The tentacles are dark, mainly at the base, and have a central white band. Tentacle tips are unpigmented. The mantle edge is also dark. On the sole of the foot there are some white granules.

Nervous System (Fig. 5B). The two cerebral ganglia are connected by a cerebral commisure and lie over the oesophagus. The right and left pleural ganglia are about the same size and rise out of the curvature of the cerebral ganglia. Seen from above, it is not possible to discern the left pleural ganglion nor the subesophageal ganglion, because at that point the oesophagus forms a curve that prevents direct observation. Once it is removed, the left pleural ganglion and the suboesophageal ganglion appear fused without any connective. The right pleural ganglion is joined to the supraoesophageal ganglion by a long connective. Nervous system measurements are: length of the right cerebral ganglia: 0.24 mm; length of the cerebral commisure: 0.08 mm; length of the right pleural ganglion: 0.08 mm; length of the left pleural ganglion: 0.10 mm; length of the supraesophageal ganglion: 0.07 mm; length of the subesophageal ganglion: 0.06 mm; length of the pleuro-supraesophageal connective: 0.15 mm. RPG ratio = 0.48.

Mantle Cavity. The mantle epithelium is pigmented uniformly black, except on the body whorl, which is less pigmented making it possible to follow the position of the intestine. The ctenidium occupies nearly the entire lenght of the pallial cavity with a variable number of well-developed lamellae. There are usually about 14, but may vary from 11 to 18 (Fig. 5C). At the base of the gill, near the neck, there is a well developed ovoid-annular osphradium.

Operculum (Fig. 4G, H, Table 2). It is corneus, paucispiral and thin. The pale yellowish nucleus is subcentral. Measurements are shown in Table 2.

Digestive System (Table 4). In the pallial cavity, the rectum forms a more or less markedly U-shaped bend beside the prostate or pallial oviduct (Figs. 5C, D, 7). It ends near the distal corner of the mantle cavity. The di-

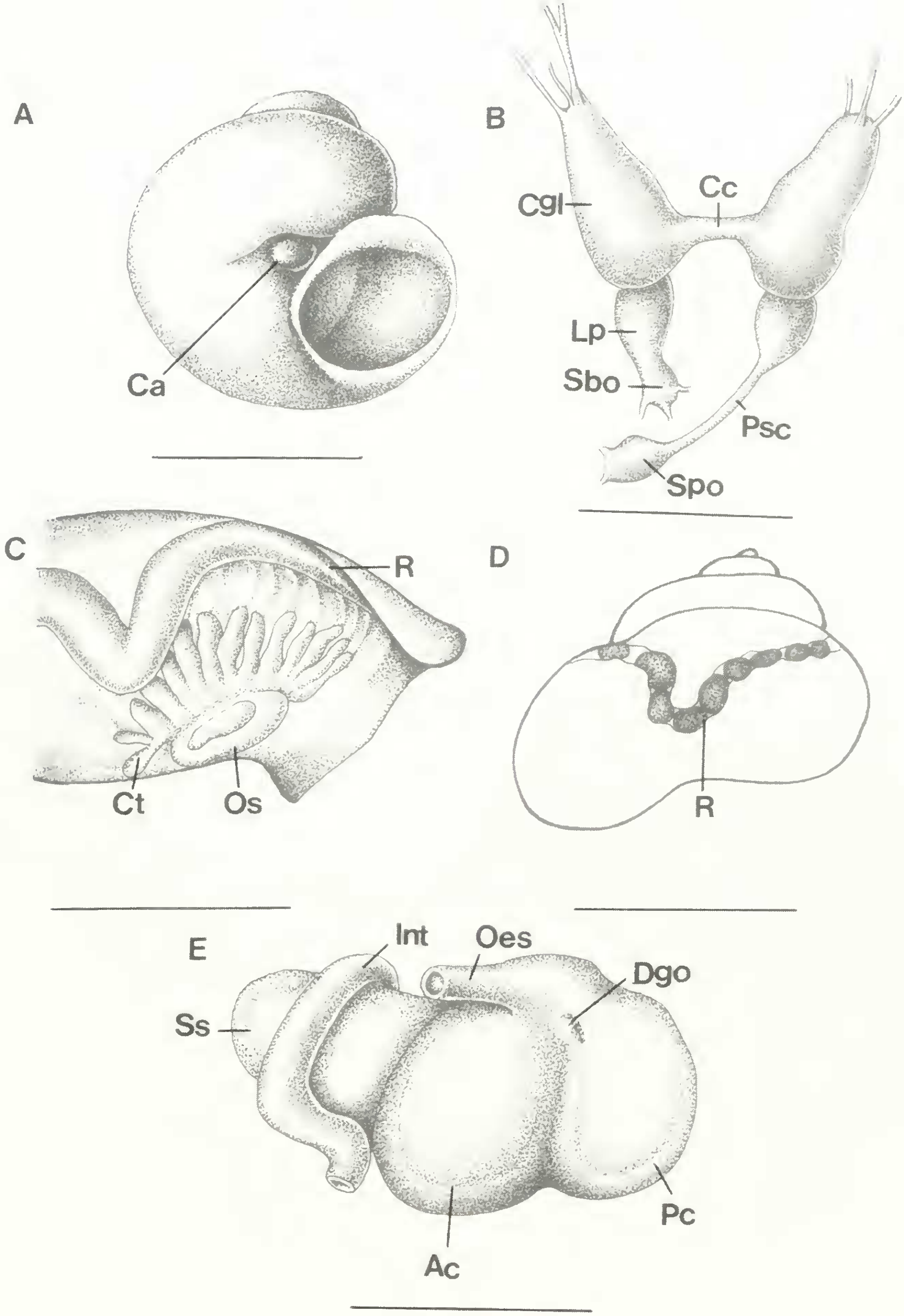

FIG. 5. Shell, nervous system, pallial organs and digestive system of *Tarraconia gasulli* from Manantial La Esperanza, Navajas, Castellón. A. Shell with an egg capsule in the umbilicus; B. Partial nervous system; C. Osphradium and ctenidium; D. Lateral view of the shell. The U-shaped intestine can be seen by transparency; E. Stomach. Scales bars: A, D: 1 mm; B: 250 μm; C, E: 500 μm. Abbreviations: Ac. anterior chamber of the stomach; Ca. capsule; Cc. cerebral commisure; Cgl. left cerebral ganglion; Ct. ctenidium; Dgo. digestive gland opening; Int. intestine; Lp. left pleural ganglion; Oes. oesophagus; Os. osphradium; Pc. posterior chamber of the stomach; Psc. pleurosupraoesophageal connective; R. rectum; Sbo. suboesophageal ganglion; Ss. style sac; Spo. supraoesophageal ganglion.

TABLE 2. Operculum measurements (in mm) of *Tarraconia gasulli* (La Esperanza, Navajas) and *T. rolani*. (La Carroba). SD = Standard Deviation, CV = Coeff. of Variation.

	T. gasulli			*T. rolani*		
	La Esperanza, Navajas			La Carroba		
Variables	Mean	S.D.	C.V.	Mean	S.D.	C.V.
OL	0.74 (n = 7)	0.11	0.14	0.73 (n = 4)	0.03	0.04
OW	0.60 (n = 7)	0.08	0.14	0.62 (n = 5)	0.03	0.04
OLWL	0.21 (n = 3)	0.05	0.22	0.22 (n = 5)	0.03	0.14
OLWW	0.18 (n = 3)	0.03	0.18	0.19 (n = 5)	0.03	0.15
NL	0.40 (n = 4)	0.09	0.23	0.35 (n = 4)	0.03	0.08
NW	0.43 (n = 4)	0.12	0.27	0.43 (n = 5)	0.01	0.02
OL/OW	1.23 (n = 7)	0.04	0.03	1.16 (n = 4)	0.02	0.01

gestive gland is continuously distributed from the posterior chamber of the stomach to the end of the body. The posterior stomach has no caecum (Fig 5E). The style sac is formed by a monostratified ciliated epithelium, with cubical cells filled with a rather dense cytoplasm in which a large rounded nucleus is centrally placed. The distal surface is densely clothed with long, close-set cilia (Fig. 9A). The stomach has two different types of epithelium. The first is a high, columnar, ciliated, monostratified epithelium with basally situated nuclei. The second is a pseudostratified ciliated epithelium. These cells are sometimes observed to be full of vesicles.

The typically taenioglossate radula has a central tooth with the usual butterfly-shaped hydrobiid structure (Fig. 6A–E). The cutting edge is markedly excavated. The apex is V-shaped, with a long middle cusp and five smaller cusps on each side that decrease in size towards the edge. The lateral wings have one cusp on each of the basal angles. The lateral teeth have slender lateral wings with one pointed basal cusp on each side. They have a large wide central cusp pointing toward the central teeth, and 4 or 5 other cusps at each side, decreasing in size. The two pairs of marginal teeth are similar in shape, the apex of the outer one being small. Both have a long row of denticles of similar size. Radular formula and measurements appear in Table 3.

Female Reproductive System. An uncoiled female snail is shown in Figure 7A. Other details in Figure 8A, B. Measurements in Table 4.

The pallial oviduct is divided into an albumen gland and a capsule gland, the border of which is not straight, but slightly lobulated. It is slightly lengthened in its anterior part. The capsule gland comprises more than half the pallial oviduct.

The bursa copulatrix clearly protrudes at the end of the pallial oviduct. It is well developed, pyriform and not ciliated. It has a long, slender anterodorsal duct and constitutes almost half the length of the pallial oviduct.

There is no seminal receptacle. The renal oviduct is unpigmented and forms a loop leaning against the pallial oviduct. The part of the coiled oviduct proximal to the bursa copulatrix is greatly thickened because of its strong columnar epithelium that makes longitudinal folds and leaves a stretched lumen (Fig. 9C). This epithelium is highly ciliated, and some of spermatozoa are arranged with their heads between the cilia and their tails projecting towards the lumen (Fig. 9D). The epithelium of the rest of the oviduct is much thinner and unciliated (Fig. 9E), very similar to that of the bursa copulatrix (Fig. 9B). In the breeding period, the lumina of both are filled with unoriented sperm. Externally, the swollen area is clearly recognisable by its refractivity, iridescent colour, and its position with regard to the oviduct loop. The mature female gonad consists of vitellogenic oocytes that have a very well-developed cytoplasm full of yolk, each measuring 120–200 µm. These yolk granules are iridescent yellow. Previtellogenic oocytes are roundish and measure approximately 30–60 µm in diameter (Fig. 9F). The sex cells are bordered by a germinal epithelium. The gonad is separated from the digestive gland by a thin layer of connective tissue. The ventral channel is ciliated.

Egg Capsule. In some specimens, an egg capsule was found inside the umbilicus with a single egg (Fig. 5A). Embryos have been found at different stages of maturation (Fig. 6F). The capsule is approximately 200 µm and can be seen in both males and females.

Male Reproductive System. An uncoiled male snail is shown in Figure 7B. Other de-

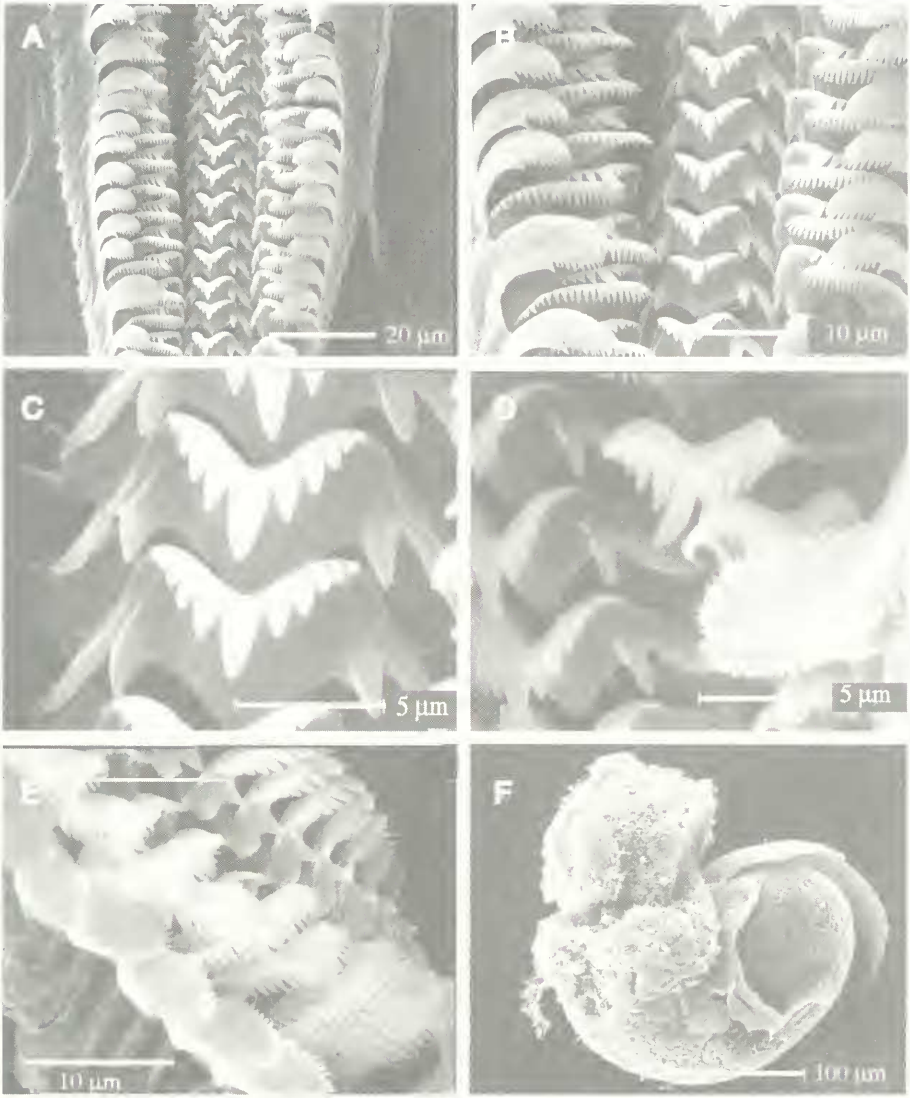

FIG. 6. A–E. SEM photomicrographs of *Tarraconia gasulli* radula from Manantial La Esperanza, Navajas, Castellón. A, B. Transverse rows; C. Central teeth; D. Central, lateral and inner marginal teeth; E. Lateral view of the central, inner and outer marginal teeth; F. Embryo before hatching after partially removing the capsule.

tails are shown in Figure 8C, D. Penis and prostate measurements are shown in Table 4.

The anterior part of the testis does not overlap the posterior chamber of the stomach. The male gonad is very well developed, and consists of multiple lobes that extend towards the end of the body whorl (Fig. 7B). Inside these lobes, maturation of the sex cells goes from the outer part to the inner part so spermatogonial cells can be found on the periphery and spermatozoids in the centre (Fig. 9G). The anterior coils of the seminal vesicle overlap the posterior chamber of the stomach. The posterior vas deferens enters the prostate gland approximately in the middle part. The vas efferens and seminal vesicle can clearly be seen because of the iridescent pink sperm. The prostate is typically bean-shaped and the lumen U-shaped. The anterior deferens vas can be seen near its anterior tip.

TABLE 3. Radula of *Tarraconia gasulli* (La Esperanza, Navajas) and *T. rolani* (La Carroba). Formula and measurements (in μm).

Variables	*T. gasulli* La Esperanza, Navajas	*T. rolani* La Carroba
Central teeth	(4)–5+C+(4)–5/1–1	5+C+5/1–1
Cutting edge width	≈7.05	≈8.3
Lateral teeth	4–5+C+4	6+C+4
Inner marginal teeth	21–25	25–28
Outer marginal teeth	11–18	14

The penis is inserted in the right middle part of the neck. It is cylindrical in the transverse section, very well developed, and has a medium-sized roundish lobe on the concave side in its central part. On histological slides, no glandular structures were seen in this lobe (Fig. 9H). The penis is slightly pigmented in its distal part below the lobe, where it narrows and finishes in a blunt tip. The narrow penis duct is straight and lies towards the right edge.

Remarks

The Segorbe population shows slight variations in shell proportions, but has the typical shell shape and marked varix behind the outer lip. The female genital system follows the pattern described for *T. gasulli,* and the penis seems to be more slender, having a smaller lobe. Its geographical location between the type locality and Navajas led us to include it as *T. gasulli* until new records are available.

Habitat and Distribution

The species seems to be restricted to a few localities in a small area in Castellón Province in the easternmost part of Spain. It lives in springs and irrigation ditches with clean water and much aquatic vegetation. In these environments, specimens can be found on the vegetation, stones or even in the mud, together with a wide variety of other freshwater molluscs, the most common being species of the genera *Pisidium, Melanopsis, Theodoxus, Belgrandia, Pseudamnicola* and *Lymnaea.* Live specimens were found in all the localities, except the type locality, most being very well preserved. In Benifaió, Valencia, only three adult specimens, one juvenile and one shell were collected. The female anatomy and shell features suggest tentatively including the Benifaió population as *T. gasulli.*

Tarraconia rolani Ramos, Arconada & Moreno, new species

Type Material

Holotype (Figs. 10A, E, F) and paratypes (Figs. 10C, G, I, 11B) (09) MNCN 15.05/33131 (ethylic alcohol material and golden SEM preparation) (30/9/1990), MNCN 15.05/33132 (in ethylic alcohol material and golden SEM preparation) (29/3/1990) (Figs. 10B, D, H, 11A, MNCN 15.05/33136 (ethylic alcohol and frozen material) (13/3/1999).

Localities

(07), MNCN 15.05/33133 (dried and ethylic alcohol material) (30/3/1990), MNCN 15.05/33134 (ethylic alcohol material) (25/7/1996) and MNCN 15.05/33137 (ethylic alcohol material) (13/11/1999).

Type Locality

Irrigation ditch on the road from San Carlos de la Rápita to Tortosa (08), La Carroba, Tarragona.

Etymology

This new species is dedicated to Dr. Emilio Rolán in recognition of his important contribution to Spanish freshwater malacological fauna.

Morphology

Shell (Figs. 10, 11A, B; Table 1). The shell is dextral, valvatoid, very small, wider (1.52–2 mm) than it is tall (1.17–1.80 mm), thin, whitish and translucent, with 3.5–4 whorls. Periostracum is yellowish. The whorls are rounded, the sutures are deep, and the body whorl occupies 5/6 parts of total shell length. The aperture close but not adhering to the last whorl, rounded, with a slight angularity close to the penultimate whorl. Its outer lip is straight, parallel to the columella or very slightly inclined backwards, with a slight varix behind the outer lip. The umbilicus is very

TABLE 4. Anatomical measurements (in mm) of *Tarraconia gasulli* (La Esperanza, Navajas) and *T. rolani* (La Carroba). SD = Standard Deviation, CV = Coefficient of Variation.

	T. gasulli			*T. rolani*		
	La Esperanza, Navajas			La Carroba		
Variables	Mean	S.D.	C.V.	Mean	S.D.	C.V.
Bc L	0.27 (n = 4)	0.04	0.16	0.32 (n = 3)	0.03	0.08
Bc W	0.19 (n = 4)	0.04	0.18	0.32 (n = 3)	0.03	0.09
DBc L	0.24 (n = 4)	0.07	0.28	0.08 (n = 3)	0.04	0.50
Po L	0.71 (n = 3)	0.05	0.07	0.66 (n = 3)	0.03	0.05
Po W	0.43 (n = 3)	0.01	0.02	0.44 (n = 3)	0.06	0.13
Ag L	0.31 (n = 3)	0.14	0.45	0.37 (n = 2)	0.02	0.06
Cg L	0.39 (n = 3)	0.09	0.24	0.27 (n = 2)	0.04	0.14
P L	1.00 (n = 6)	0.24	0.24	1.61 (n = 4)	0.45	0.28
P W	0.14 (n = 6)	0.04	0.30	0.14 (n = 4)	0.03	0.19
Pr L	0.52 (n = 2)	0.08	0.15	0.70 (n = 3)	0.07	0.62
Pr W	0.25 (n = 2)	0.10	0.41	0.38 (n = 3)	0.05	0.14
Pl L	0.17 (n = 4)	0.03	0.20	0.15 (n = 4)	0.03	0.22
Pl W	0.22 (n = 6)	0.05	0.22	0.20 (n = 4)	0.04	0.22
P L/Head L	1.31 (n = 5)	0.43	0.33	2.13 (n = 4)	0.75	0.35
Os L	0.21 (n = 5)	0.09	0.42	0.29 (n = 5)	0.05	0.18
Os W	0.12 (n = 5)	0.03	0.29	0.14 (n = 5)	0.03	0.23
Ct L	0.64 (n = 5)	0.26	0.41	0.62 (n = 5)	0.14	0.23
Ct W	0.15 (n = 5)	0.04	0.29	0.16 (n = 5)	0.02	0.12
Ss L	0.33 (n = 5)	0.04	0.13	0.45 (n = 5)	0.07	0.15
Ss W	0.20 (n = 5)	0.03	0.16	0.32 (n = 5)	0.05	0.15
St L	0.41 (n = 5)	0.09	0.23	0.59 (n = 4)	0.17	0.28
St W	0.32 (n = 5)	0.03	0.11	0.45 (n = 4)	0.09	0.20

wide, around 0.33 mm, about 1/5 of shell diameter.

The protoconch is clearly differentiated from the teleoconch (Fig. 11A, B). The external surface of the protoconch is wrinkled, with smoothly pitted sculpture. It has 1.5 whorls. Total width (PW) is about 0.34 mm and the width of the nucleous (PNW) approximately 0.12 mm. The teleoconch is smooth, with fine and regular growth lines.

External Body Features. The head is pigmented brown, but the pigment fades towards the snout, which is totally unpigmented, allowing observation of the radular sac. The tentacles are dark, mainly at the base, and have a central white band (Fig 12C). Tentacle tips are unpigmented. The mantle edge is also dark. There are a few white granules on the sole of the foot.

Nervous System (as in *T. gasulli*). The two cerebral ganglia are connected by a cerebral commisure and lie over the oesophagus. The right and left pleural ganglia are about the same size and rise out of the curvature of the cerebral ganglia. The right pleural ganglion is connected with the supraoesophageal ganglion by a long connective. Nervous system measurements are: length of the right cerebral ganglia: 0.17 mm; length of the cerebral commisure: 0.05 mm; length of the right pleural ganglion: 0.09 mm; length of the left pleural ganglion: 0.10 mm; length of the supraesophageal ganglion: 0.09 mm; length of the subesophageal ganglion: 0.08 mm; length of the pleurosupraesophageal connective: 0.10 mm. RPG ratio = 0.39.

Mantle Cavity. The mantle epithelium is pigmented uniformly brown, except on the body whorl, which is less pigmented, making it possible to follow the position of the intestine. There is a well-developed ctenidium, with the number of lamellae varying from 11 to 16, but usually about 14. At the base of the gill, near the neck, there is a well-developed ovoid annular osphradium.

Operculum (Fig. 11C–E, Table 2). Operculum corneus, paucispiral, thin. The pale yellowish nucleus is in a subcentral position on the operculum.

Digestive System. The stomach and style sac, although similar in overall shape, differ in size and proportion from those of *T. gasulli* (Table 4). The rectum forms a markedly U-shaped bend, sometimes directed towards the mantle border. It ends near the distal corner of the mantle cavity.

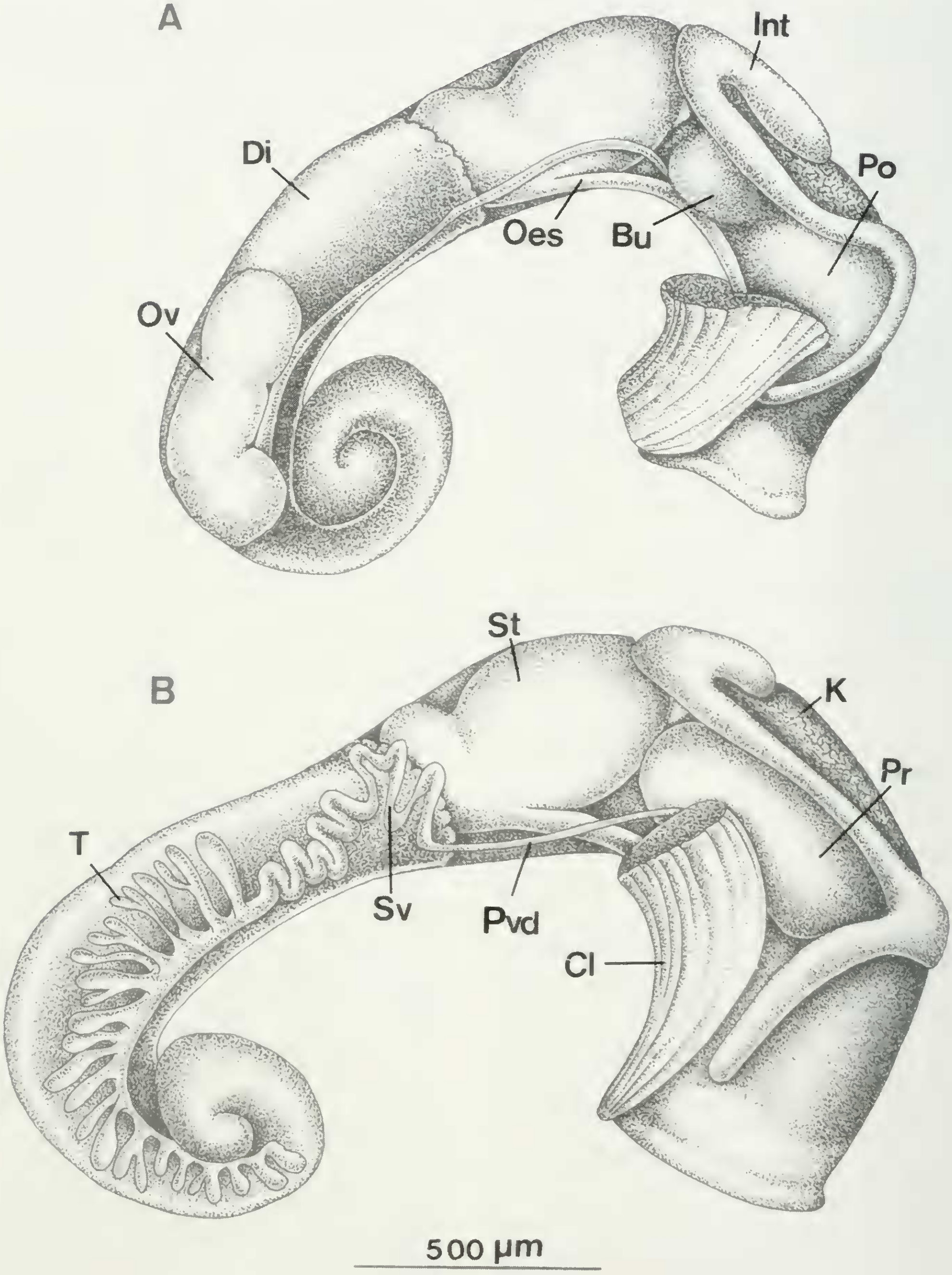

FIG. 7. A. Uncoiled bodies without head of A. female and B. male of *Tarraconia gasulli*. Abbreviations: Bc. bursa copulatrix; Cl. columellar muscle; Di. digestive gland; K. kidney; Int. intestine; Oes. oesophagus; Ov: ovary; Pg: paleal gland; Pr. prostate; St. stomach; Sv. seminal vesicle; T. testis; Pvd. posterior vas deferens.

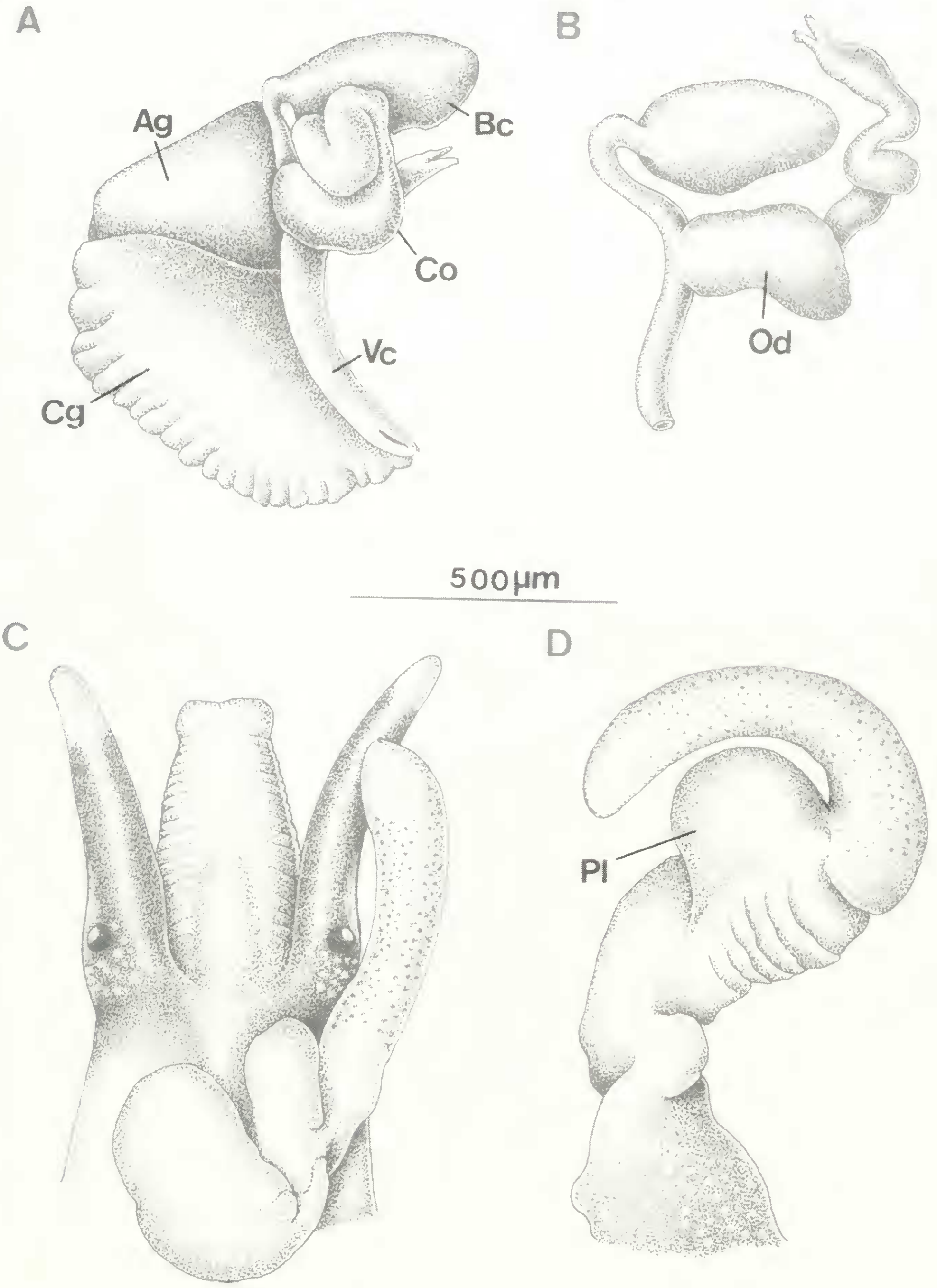

FIG. 8. Female and male genitalia of *Tarraconia gasulli* from Manantial La Esperanza, Navajas, Castellón. A, B. Anterior female genitalia (note the enlargement of the oviduct); C, D. Head of a male and penis. Abbreviations: Ag. albumen gland; Bc. bursa copulatrix; Co. coiled part of the oviduct; Cg. capsule gland; Od. oviduct; Pl. penial lobe; Vc. ventral channel.

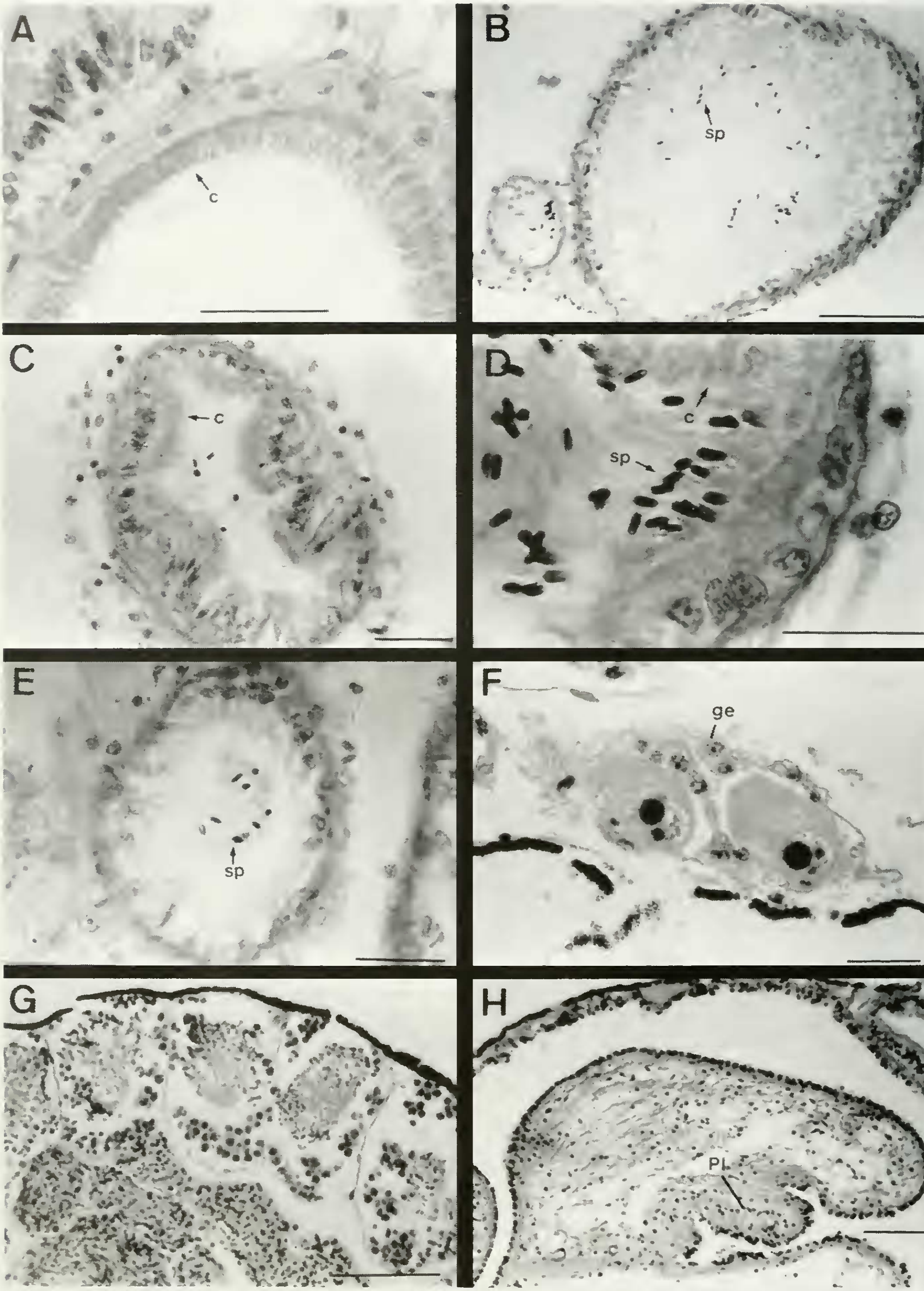

FIG. 9. Histological sections of *Tarraconia gasulli* from Manantial La Esperanza, Navajas, Castellón. A. Epithelium of the style sac; B. Bursa copulatrix and duct; C. Thickened part of the oviduct (note narrow lumen); D. Heads of the spermatozoids attached to the ciliated epithelial cells of the thickened oviduct; E. Oviduct not enlarged (note spermatozoids in lumen); F. Previtellogenic oocytes; G. Male gonadal lobes; H. Penis and lobe. Abbreviations: c. cilia; ge. germinal epithelium; sp. spermatozoids; Pl. penial lobe. Scale bar: A, C, D, E, F: 25 μm; B, G, H: 0.1 mm.

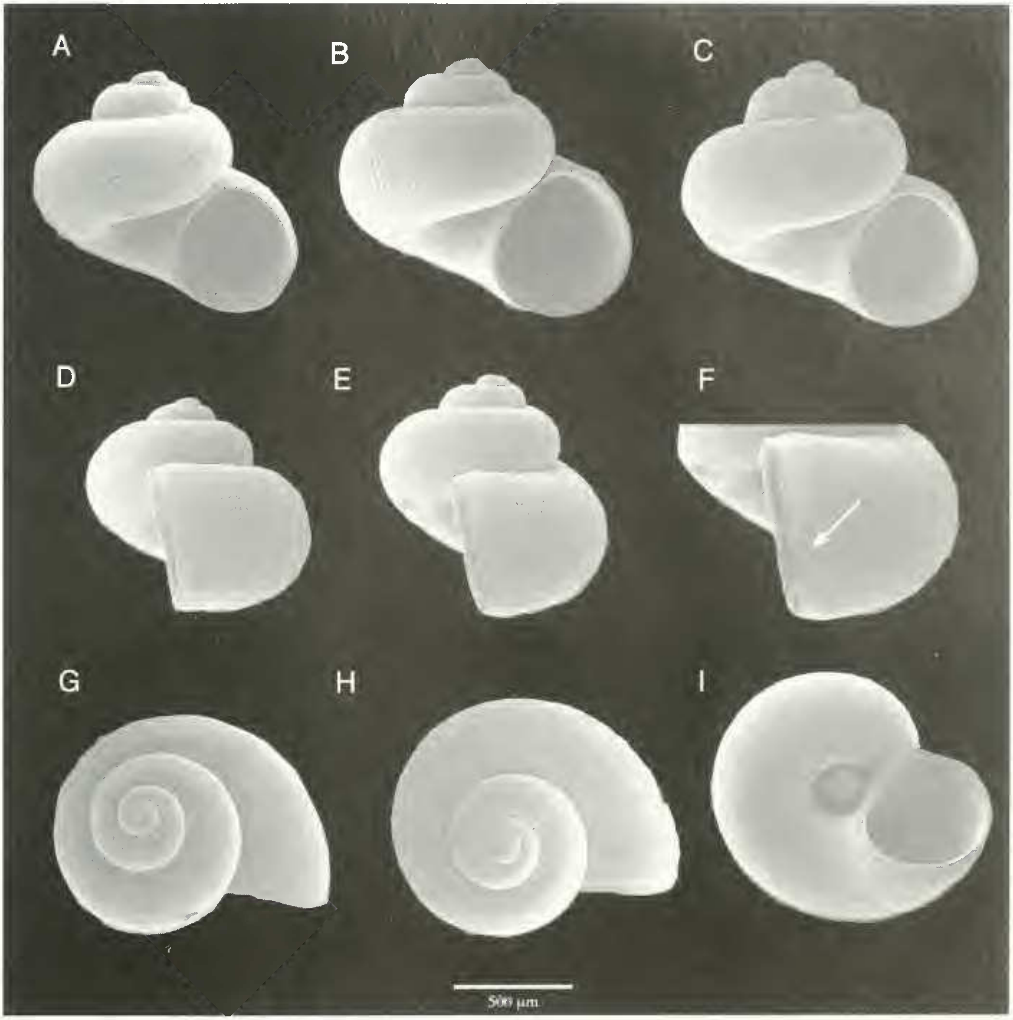

FIG. 10. SEM microphotographs of *Tarraconia rolani* shells from the type locality (La Carroba, Tarragona). A, E, F. Holotype. B, C, D, G, H, I. Paratypes. The arrow in Fig. F indicates the slight varix behind the outer lip. (note the embryo inside the umbilicus in Fig. I).

The radula is typically taenioglossate. The total size of radular ribbon is 0.45 µm and is medium-sized relative to mean shell dimension (Fig. 12A) (Hershler & Ponder, 1998). The central tooth, with the usual butterfly-shaped hydrobiid structure, has a slightly excavated cutting edge (Fig. 12B–D). The apex is V-shaped with a long middle cusp and five smaller cusps on each side that decrease in size towards the edge (Fig. 12C). The lateral wings have one cusp on each of the basal angles. The lateral teeth have slender lateral wings with one pointed basal cusp on each side. They have a large wide central cusp that points toward the central teeth, and 4 to 6 other cusps at each side, decreasing in size (Fig. 12C–E). The two pairs of marginal teeth have a long row of denticles of similar size (Fig. 12E–F). Radular formula and measurements are given in Table 3.

Female Reproductive System (Fig. 13A, B, Table 4). The pallial oviduct is sometimes slightly lengthened in its anterior part. The capsule gland is about 1/3 the pallial oviduct. The bursa copulatrix protrudes at the end of the pallial oviduct. It is well developed,

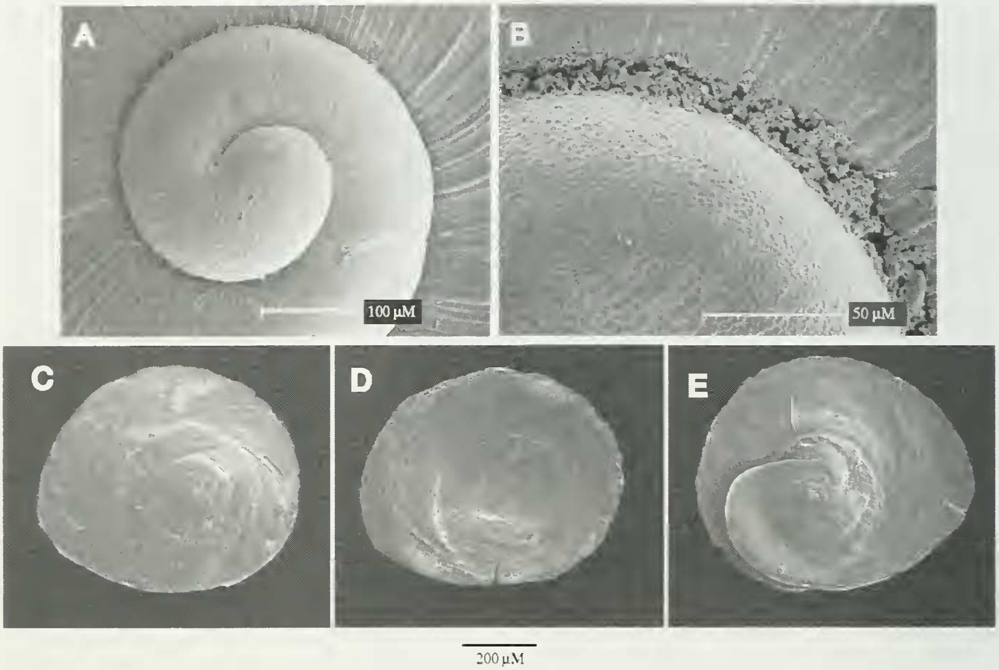

FIG. 11. SEM photomicrographs of *Tarraconia rolani* protoconch and opercula from the type locality (La Carroba, Tarragona). A, B. Protoconch; C, D, E. Outer and inner side of the opercula.

roundish, has a short duct and constitutes half the length of the pallial oviduct. The renal oviduct is unpigmented and forms a wide loop leaning against the pallial oviduct.

Egg Capsule. Several specimens were observed to be carrying a single egg capsule inside the umbilicus with an embryo at different stages of maturation (Fig. 10I).

Male Reproductive System (Fig. 13C, D, Table 4). The posterior vas deferens enters the prostate gland approximately in the middle part. The vas efferens and seminal vesicle can clearly be seen because of the iridescent pink sperm. The prostate is oval or bean-shaped and the lumen U-shaped. The anterior deferens vas can be seen near its anterior tip.

The penis is inserted in the right middle part of the neck. It is cylindrical in the transverse section, very long and slender, and has a small lobe on the concave side in its central part that looks like a tip and forms a 90° angle to the central axis of the penis. The penis is not pigmented in its distal part below the lobe, where it narrows and tapers at the end. The narrow penis duct is straight and lies towards the right edge.

Remarks

This species differs from *T. gasulli* in a set of character states as follows: shell shape (wider than taller), a much slighter varix behind the outer lip, the shape of the cutting edge of the central teeth, overall shape of the bursa copulatrix, shorter duct of the bursa copulatrix, penis size, overall shape of the penis lobe, tapered shape of penis tip, lack of pigmentation on the penis, and size and shape of the anterior digestive system. External pigmentation appears lighter than in *T. gasulli*.

Habitat and Distribution

The species seems to be restricted to a few localities in a small area in Tarragona province. It lives in springs and irrigation ditches with clean water and much aquatic vegetation. In these environments, it can be found on

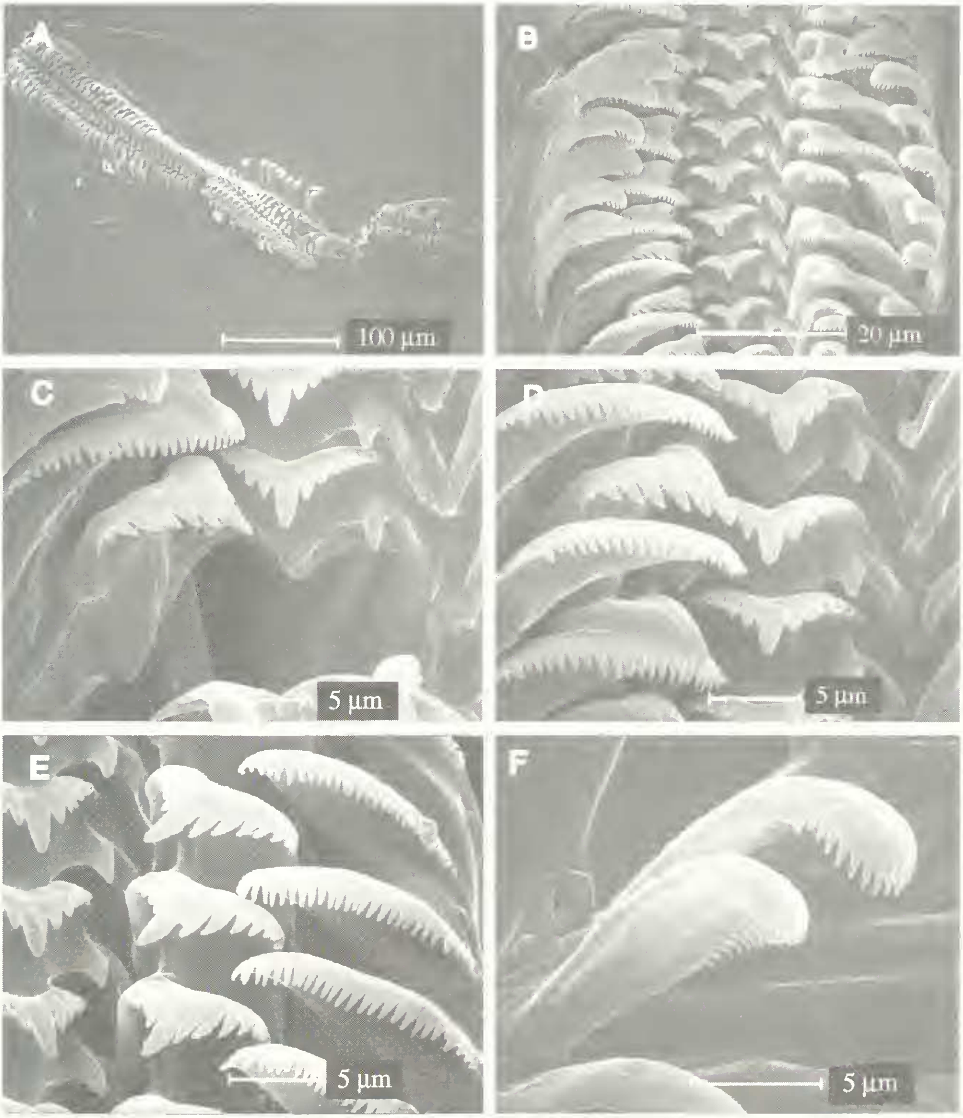

FIG. 12. A–E. SEM photomicrographs of *Tarraconia rolani* radula from the type locality. A. Complete radula. B. Transverse rows. C. Central and lateral teeth. D, E. Central, lateral and inner marginal teeth. F. Outer marginal teeth.

the roots of the vegetation, stones or even in sand and other artificial substrata with a wide variety of other freshwater molluscs, the most common being species of the genera *Pisidium, Melanopsis, Theodoxus, Belgrandia, Pseudamnicola, Potamopyrgus, Ferrisia, Lymnaea* and *Physa*. Live specimens were found in all localities except the type locality, most being very well preserved.

STATISTICAL ANALYSIS AND MORPHOLOGICAL DIFFERENTIATION BETWEEN SPECIES

Variation in shell measurements in the three study populations can be seen in Tables 1 and 5 and Figures 14 and 15. The t-values for the anatomical data and the significance level are shown in Table 7.

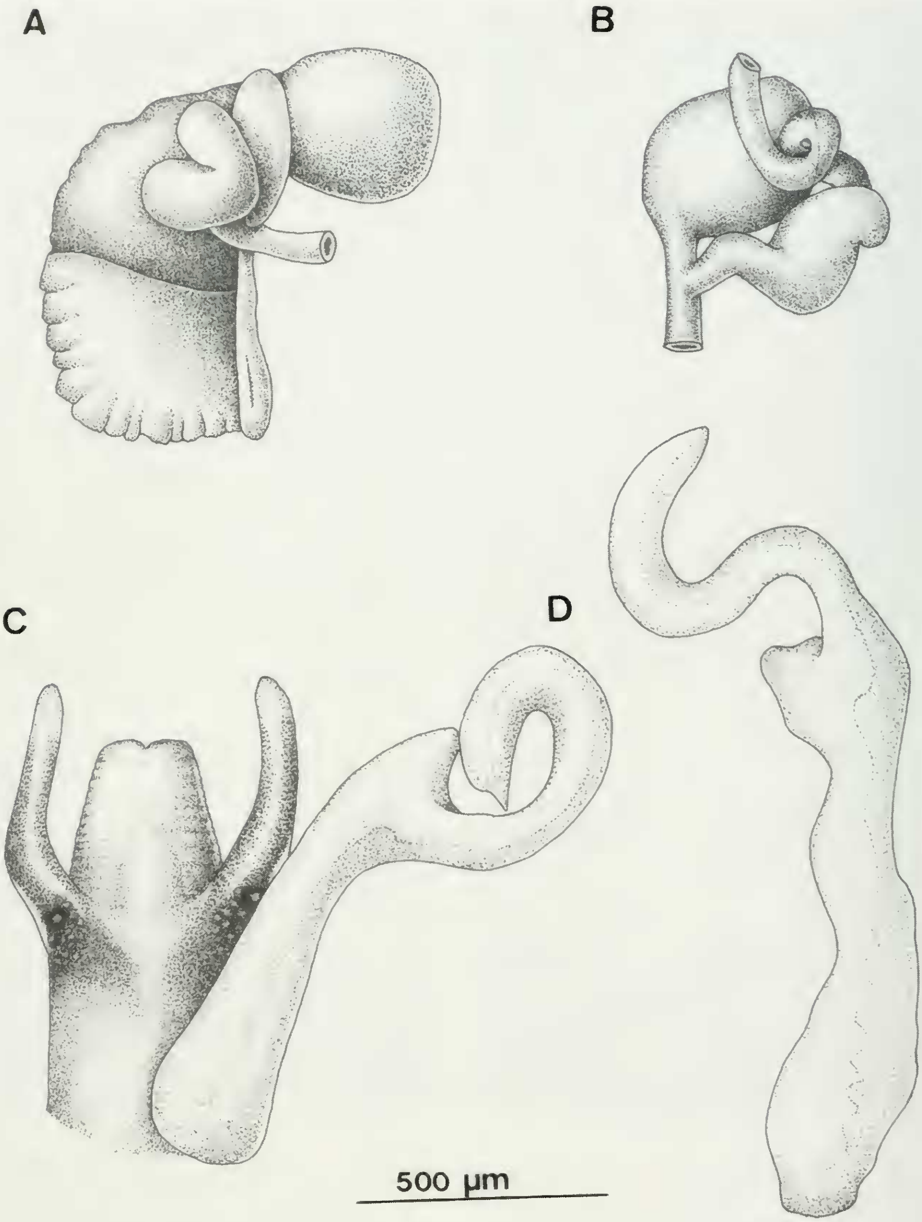

FIG. 13. Female and male *Tarraconia rolani* genitalia. A, B. Anterior female genitalia (note the enlargement of the oviduct); C, D. Head of a male and penis.

On the basis of shell characters (the only characters available both from type material and topotypes collected at the type locality of *T. gasulli*), the ANOVA (Table 6) demonstrated that the live specimens collected in the neighbouring locality, Manantial La Esperanza, clearly belong to *T. gasulli*. The only differences between both populations are the number of spire whorls (NSW) and the width of the antepenultimate whorl (WAW). In addition, ANOVA showed significant differences between *T. gasulli* and *T. rolani* for some of the most important conchological variables studied. These differences are related to shell

TABLE 5. F-values of the Anova statistical analysis for shell variables and differences between populations resulting from the Scheffé Test. POP. 1: *T. gasulli* (La Esperanza, Navajas). POP. 2: *T. gasulli* (El Bañador, Altura). POP. 3: *T. rolani* (La Carroba).

Variables	F (2,74)	POP. 1	POP. 2	POP. 3
SL	14.550***	3	3	1,2
SW	16.296***	3	3	1,2
AH	0.583*			
LBW	24.572***	3	3	1,2
WBW	2.639*			
AmL	1.505*			
AmW	2.341*			
WPW	4.597**	3		1
WAW	8.777***	2,3	1	1
NSW	5.611**	2,3	1	1

length (SL) and width (SW), length of body whorl (LBW), and width of the penultimate whorl (WPW). Mean WPW values only differ between Altura (type locality of *T. gasulli*) and La Carroba (type locality of *T. rolani*) populations, but not between both *T. gasulli* populations. Two variables, the width of the antepenultimate whorl (WAW) and the number of spire whorls (NSW), differ between *T. gasulli* (type locality) and the rest. Aperture height (AH), width of body whorl (WBW) and aperture length and width (AmL, AmW) are not useful variables to investigate differences between the two species. All the above suggests that the variables that most contribute to shell shape are those that are most different between *T. gasulli* and *T. rolani* n. sp.

Differences between species were also confirmed by the DFA. Two highly significant discriminant functions were found (Wilk's lambda = 0.102, F (10,134) = 28.458, $p < 0.001$) for shell characters. The variables included in both functions were: LBW, SW, SL, AmW and WAW. For the first function, which accounted for 82% of explained variance, the characters that contribute (highest weight) were (in order): LBW, AmW, SW, WAW and SL. For the second function, the order was: LBW, SL, SW, WAW, AmW. Both discriminant functions were highly significant ($p < 0.001$). The classification functions being: El Bañador, Altura: [f1 = $-117.179 + (95.665 \times \text{LBW}) + (49.806 \times \text{SW}) + (67.485 \times \text{SL}) + (185.587 \times \text{AmW}) + (39.565 \times \text{WAW})$]. La Esperanza, Navajas: [f2 = $-128.328 + (147.123 \times \text{LBW}) + (66.343 \times \text{SW}) + (104.885 \times \text{SL}) + (8165.244 \times \text{AmW}) + (6.515 \times \text{WAW})$]. LaCarroba: [f3 = $-142.381 + (21.809 \times \text{LBW}) + (91.157 \times \text{SW}) + (-77.679 \times \text{SL}) + (261.688 \times \text{AmW}) + (71.541 \times \text{WAW})$].

Seventy nine percent of variance from the statistical data was due to interpopulational variation. On the scatterplot, three clusters can be observed, two of them overlapping and corresponding to the two *T. gasulli* study populations. The third, which is separated and does not overlap, corresponds to *T. rolani*. From the total data, 75% of cases were correctly assigned to *T. gasulli* (type locality). The percentage increased to 96% for Manantial La Esperanza (Navajas) and to 92% for the *T. rolani* type locality.

The opercula variables did not present significant differences among the three study populations, not being, therefore, informative in differentiating species.

Study of the anatomical characters statistically confirmed the aforementioned differences between both species (Table 7). Two female genitalia variables presented significant differences: bursa copulatrix width (BcW) and length of the bursa copulatrix duct (DBc L). Among male genitalia variables studied, penis length (PL) was significantly longer in *T. rolani* n. sp. Differences in non-genital system variables were mainly related to the size and shape of the digestive system: style sac length (Ss L), style sac width (Ss W) and stomach width (St W).

GENERIC DIFFERENTIATION

Boeters (in Gasull, 1981) described *Hauffenia (Neohoratia) gasulli* as: "*Concha valvatiforme, cónica, con aprox. 3.5 vueltas de espira. La boca en la penúltima vuelta permanece en la misma línea, ni más alta ni más baja. Peristoma cortante, no ensanchado, algo circular, solamente algo hinchado por encima, y situado directamente en la penúltima vuelta, por lo que el ombligo queda totalmente abierto. El tuberculito, bien visible, cae detrás del borde del peristoma. Altura de la concha aprox. 1.5 mm y diámetro aprox. 106 mm*)" (shell diameter was surely a typographical mistake, which should have read 1.6 mm). These characters, the lack of information about soft parts and some differences regarding the other *Neohoratia* species led him to doubt the allocation of the species to the genus *Neohoratia* (Boeters, 1988). The set of character/character-states resulting from the addition of the anatomical data confirms that the species studied does not fit the description of any of the valvatoid genera de-

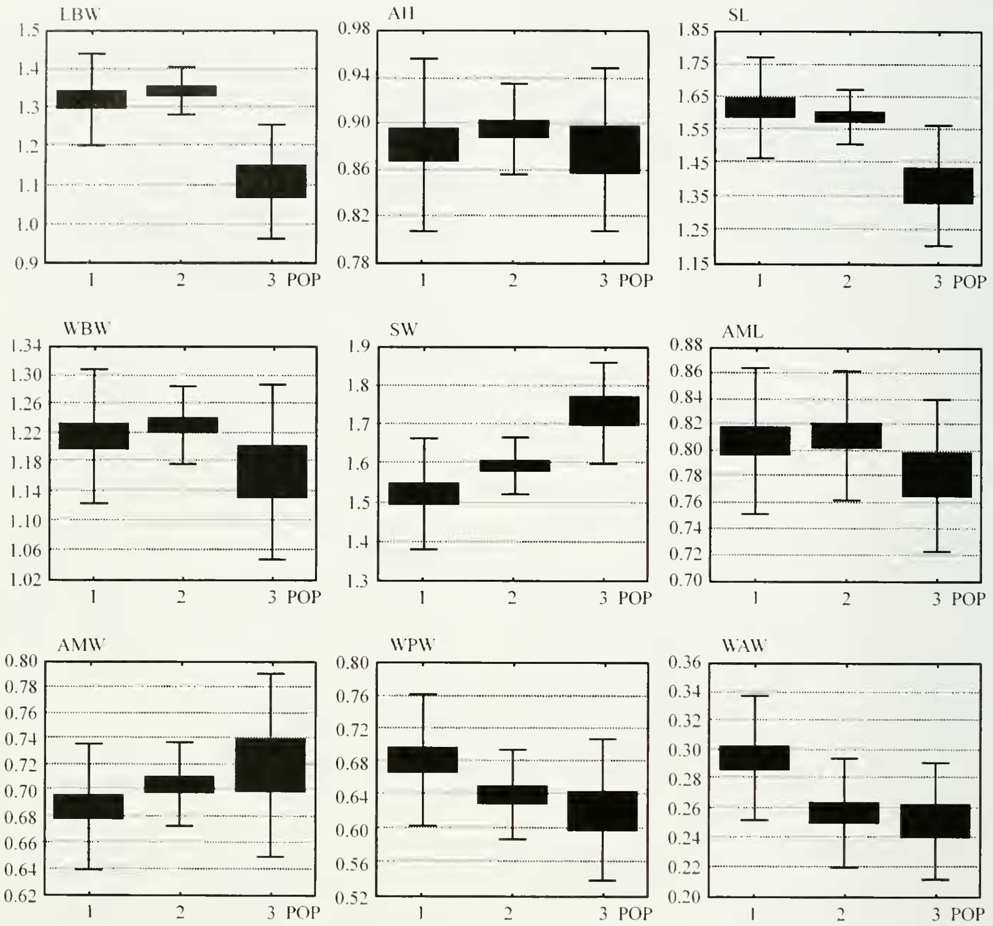

FIG. 14. Box-Whisker plots showing variation in shell measurements for the three populations considered. Pop. 1: type locality (*T. gasulli*). Pop. 2: La Esperanza, Navajas (*T. gasulli*). Pop. 3: La Carroba (*T. rolani*). Mean/SE/SD are represented.

scribed in Europe, and justifies the introduction of a new genus (Table 7).

Hauffenia is a controversial genus as can be deduced from the description of the "*Hauffenia* group" from the Balkan Peninsula (Radoman, 1978): "a group of minute subterranean forms (white or colourless) that is homogenous in shell shape, but very heterogeneous in anatomical structure". After Radoman (1983) *Hauffenia* is characterised by having a valvatiform shell, a peg-bearing operculum, two basal cusps in the central teeth, absence of RS1, but presence of a RS2, a small bursa copulatrix not protruding from the albumen gland, anterior origin of the bursal duct, and a broad penis. All these characters, except shell shape, differ from those of the new taxon.

Six species of *Neohoratia* have been described on the Iberian Peninsula (Boeters, 1988), two of them, *N. (?) gasulli* and *N. (?) fezi* (Altimira, 1960), are known only from shell characters. The anatomically known *Neohoratia* species differ from the new taxon in the lack of a bursa copulatrix, the existence of two well-developed seminal receptacles, their oviduct not being wide and the penis lobe being larger and situated in a terminal position.

Finally, in relation to the genus *Horatia* Bourguignant, 1887, which also has species on the Iberian Peninsula, the new taxon differs in shell characters, but mainly in anatomy. Species of this genus usually have two seminal receptacles, an anteroventral origin of the bursal duct, a very extended simple penis with

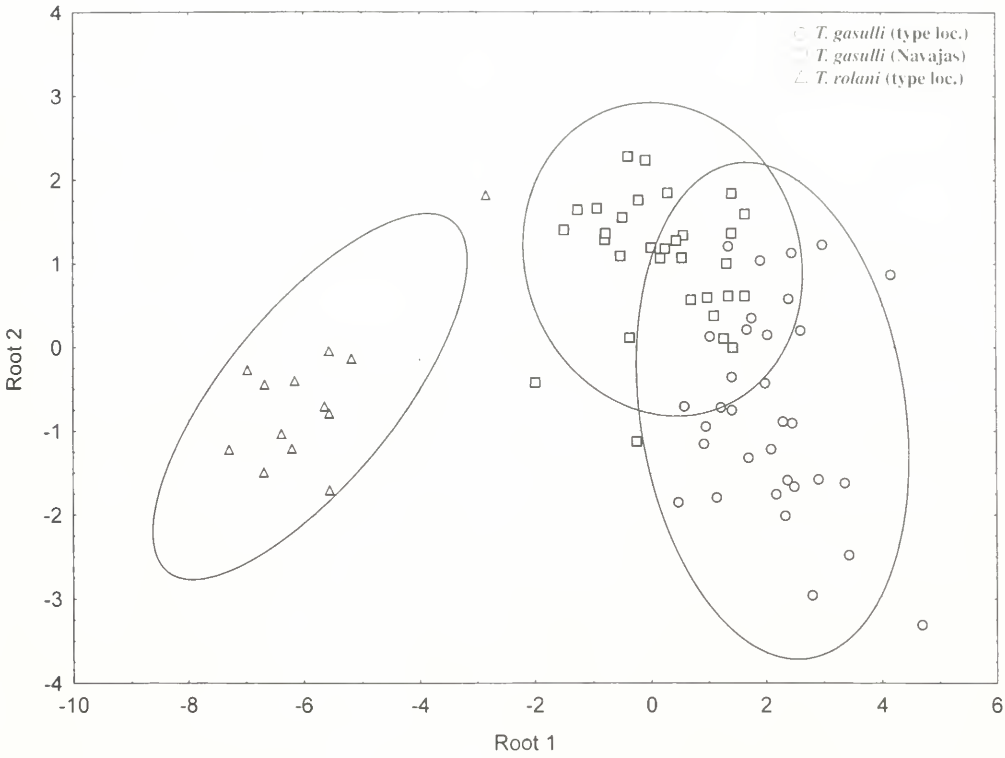

FIG. 15. Plot of discriminant scores on the two canonical axes, obtained from DFA of shell measurements for *T. gasulli* and *T. rolani* for the three populations considered. Confidence interval for ellipses: 0.95.

TABLE 6. t-values of anatomical variables for *Tarraconia gasulli* (La Esperanza, Navajas) and *T. rolani* (La Carroba). * n.s.; ** $p < 0.05$; *** $p < 0.001$.

	t-value	(df)		t-value	(df)		t-value	(df)
Os L	1.399*	(8)	Bc L	1.555*	(5)	P L	2.776**	(8)
Os W	0.639*	(8)	Bc W	5.149**	(5)	P W	–0.134*	(8)
Ct L	–0.187*	(8)	DBc L	–3.433**	(5)	Pr L	2.566*	(3)
Ct W	0.438*	(8)	Po L	–1.532*	(4)	Pr W	1.845*	(3)
Ss L	3.101**	(8)	Po W	0.261*	(4)	Pl L	–1.266*	(6)
Ss	4.447**	(8)	Ag L	0.512*	(3)	Pl W	–0.935*	(8)
St L	1.962*	(7)	Cg L	–1.697*	(3)	Head L	–0.534*	(7)
St W	2.852**	(7)						

one or two small excrescences on the left side, more than one basal cusp in the central teeth and a long suboesophageal connective.

The new genus, *Tarraconia*, is characterised by a female genital tract with a well-developed and protruding bursa copulatrix, but lacks a distinct sac-like seminal receptacle, its function being undertaken by a greatly thickened portion of the oviduct, proximal to the bursa copulatrix duct. This is suggested by the columnar ciliated epithelium, which differs from the rest of the oviduct and the bursa copulatrix, and by the orientated sperm not found in the other structures, which is the typical method of sperm storage in the seminal receptacle (Fretter & Graham, 1994: 303–306). The presence of an egg capsule in the umbilicus of *T. gasulli* is described for the first time in a hydrobiid valvatoid species in Spain. This character has been observed in other populations of wide-umbilicated valvatoid hydrobiid species from the Iberian Peninsula (unpublished data).

The lack of a seminal receptacle has been reported in some other genera of Hydrobiidae that present different anatomical strategies to

TABLE 7. Character and character-state scores for 13 characters and 6 genera. *Tarraconia*, n.g., is compared with the valvatoid-hydrobid genera mentioned for Spain, and with other genera having a similar female genital feature for Character 2. Character states have no phylogenetical significance.

Character and character-states	*Hauffenia*	*Horatia*	*Neohoratia*	*Tarraconia*	*Moitessieria*	*Trochydrobia*
Female Reproductive System						
1. Bursa copulatrix: absent (0), small (1), well developed (2)	1	2	0	2	2	2
2. Position of the bursa copulatrix relative to the albumen gland: not protruding (0), protruding (1), absent (2)	0	1	2	1	1	0
3. Origin of the bursal duct: anterior (0), anteroventral (1), anterodorsal (2), posterior (3), absent (4)	0	1	4	2	3	?
4. Seminal receptacle: RS1 (0), RS2 (1), RS1 + RS2 (2), lost with function moved within coiled oviduct (3), lost with function moved to a swollen part of posterior ventral channel of capsule gland (4)	1	0,2	2	3	3	3,4
Male Reproductive System						
5. Penis: simple (0), unilobed (1), bilobed (2)	0	1,2	1	1	0,1	0
6. Penis with lobe (s): no lobes (0), concave edge (1), convex edge (2)	0	1	1	1	0,2	0
Radula						
7. Central tooth lateral wings: with one basal cusp (0), one to three basal cusps (1)	1	1	1	0	0	1
Ctenidium						
8. Gill filaments: slightly developed (0), well developed (1), absent (2)	0	1,2	1	1	1,2	0
Rectum and Stomach						
9. Without making any loop (0), slightly sinuous (1), strongly sinuous (2)	2	1	1,2	1	1,2	1
Nervous system						
10. Suboesophageal connective: short or absent (0), long (1)	?	1	0,1	0	1	0
Shell						
11. Shape: elongated cylindro-conical (0), valvatoid (1)	1	1	1	1	0	1
12. Umbilicus: narrow (0), wide (1)	1	1	1	1	0	1
Operculum						
13. Operculum: simple (0), peg-bearing (1)	0,1	0	0	0	0	0
Sources (*)	ABC DEF	GHI	DIN	L	JM	K

(*) Sources: (A) Haase, 1992; (B) Bernasconi, 1975; (C) Bole, 1970; (D) Bole, 1967; (E) Haase, 1993; (F) Giusti & Pezzoli, 1980; (G) Radoman, 1966; (H) Radoman, 1983; (I) Boeters, 1988; (J) Bodon & Giusti, 1991; (K) Ponder et al., 1989; (L) This paper; (M) Boeters, 1973; (N) authors' unpublished data.

fulfil its function. In the genus *Moitessieria* Bourguignat, 1863 (Hydrobiinae) (Bodon & Giusti, 1991), sperm storage seems to be located in several portions of the oviduct instead of being concentrated in only one portion, as histological evidence demonstrates for *T. gasulli*. *Moitessieria* is a well-defined genus with characters that as a whole differ widely from *Tarraconia*, n. g. (Table 7). In short, it has elongated cylindro-conical shells with characteristic net-like teleoconch microsculpture, a narrow umbilicus, a posterior origin of the bursal duct, a conical, smooth, point-tipped penis with, sometimes, small glandular excrescences that are apical on the right side, and a long suboesophageal connective.

Trochydrobia Ponder, Hersler & Jenkins, 1989, described from Australia, is another valvatoid genus of Hydrobiidae lacking a seminal receptacle. In *Trochydrobia*, the role of the seminal receptacle is played by a swollen part of the posterior ventral channel of the capsule gland or in the coiled oviduct. Moreover, *Trochydrobia punicea* Ponder, Hersler & Jenkins, 1989, has a thickened coiled oviduct similar to that described for *Tarraconia*, and egg capsules in the umbilicus, as in *T. gasulli*. However, according to Ponder et al. (1989), in spite of the similarities between this species group and the European *Horatia-Pseudamnicola* complex, they have several distinct features (Table 7), such as a simple penis, a very well-developed albumen gland with a bursa copulatrix not protruding from it, up to two pairs of basal cusps in the central tooth of the radula, and a rectum that runs close to the pallial oviduct and prostate without making any loop.

Other groups of species without the seminal receptacle are included in the family Pyrgulidae, in which glandular structures, such as an oviduct with a blunt beak-shaped dilatation or a pouch-like dilatation or simply a glandulous oviduct loop without dilatation, can be found instead of the seminal receptacle (Radoman, 1983). The species belonging to this family differ from all the others described here in the glandular origin of this structures. In addition, all the genera in this clade differ in the most important characters, that is, they have an oesophageal caecal chamber and a radular central tooth without basal cusps and without the typical lateral wings of the Hydrobiinae.

The genus *Gammatricula* Davis, Liu & Chen, 1990, was introduced to isolate two species of Pachydrobiini (Triculinae, Pomatiopsidae) from China that have this female character with the same shape and position in the oviduct as described for *Tarraconia,* n. g.

In an investigation of the phylogenetic relationships of the new genus *Tarraconia* with the aforementioned genera of Hydrobiidae using PAUP 3.1 (Swofford, 1993), only 8 of the 13 characters (all characters treated as unordered and unweighted) for which enough bibliographical data were available proved to be informative (characters 2,4–10). Cladistic analysis yielded three not fully resolved trees (22 steps, C.I. = 0.66). It is well known that cladistic methodology, mainly based on establishing phylogenetic relationships through synapomorphies, is hard to achieve when few characters are available or when there is a high degree of homoplasy. Two main reasons account for the lack of available morphological characters in the case of hydrobiids: (1) the minute size results in a very few diagnostic characters and a high degree of convergence between different taxa, and (2) most European valvatoid hydrobiid genera have scarcely been studied and very few characters are available for phylogenetic inferences. In this case, the lack of data particularly affects the genera *Hauffenia* and *Horatia*. Moreover, most of the characters compared in suprageneric classifications in hydrobiids (Ponder & Warén 1988; Davis et al., 1982; Hershler, 1985) cannot be used when comparing genera or species. The few phylogenies done in this sense show a high degree of homoplasy in some of the most currently used characters of shell and genital systems (Ponder et al., 1993).

The preliminary phylogenetic analysis showed hardly any conflict among the observed characters, although its validity is uncertain due to the low number of available data sets. The absence of a seminal receptaculum, its function being transferred to the renal oviduct, is one of the most important characters of this new genus. Nevertheless, the fact that the function of a lost evolutionary character has been taken up by similar structures in different and separated taxa, even belonging to different families (Hydrobiidae, Pyrgulidae and Pomatiopsidae), suggests that it could be another case of parallel derived change. This argument seems to support Bodon & Giusti's (1991) hypothesis that the family Moitessieridae, whose isolation as a family was mostly based on this female anatomical character (Boeters, 1973), should only be considered as a junior synonym of Hydrobiidae. Nevertheless, while the obscure phylogenetic relationships of this family are being unravelled on the basis of well-founded data sets, it is clear that the description of new taxa might be based not only on one character, but on a set of characters, with as much detail as possible. Progressively thorough knowledge of the European hydrobiid fauna will help in tracing the evolution of characters.

ACKNOWLEDGEMENTS

We are indebted to Dr. G. M. Davis for his teaching and advice at the beginning of the project and for his useful suggestions concerning the manuscript. Dr. M. Haase and an anonymous reviewer made very useful and constructive comments. We thank Dr. R. Araujo, J. Bedoya, J. M. Remón, Dr. G. Tapia, Dr. C. Noreña and N. Martín for providing us with field samples. Dr. J. Lobo provided statistical advice. Histological sections were made by J. Cabanillas. SEM photomicrographs were made by J. Bedoya at the MNCN. Drawings were re-done by I. Díaz-Cortaberría. Advice on nomenclature was provided by Dr. M. A. Alonso-Zarazaga. The English was corrected by L. Ashcroft. This work was supported by the "Fauna Ibérica" Project (DGES PB95-0235).

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Revised ms. accepted 22 June 1999